# ON THE AFFINITIES OF TWO INTERESTING FOSSIL INSECTS FROM THE UPPER CARBONIFEROUS OF COMMENTRY, FRANCE.

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(With three Text-figures).

In May, 1917, Mr. Herbert Bolton, M.Sc., F.R.S.E., F.G.S., Director of the Bristol Museum, England, published an interesting paper upon the "Mark Stirrup" Collection of Fossil Insects from the Coal-Measures of Commentry (Allier), Central France.* As is well known, these insect-beds are of Upper Carboniferous Age, and have yielded a very large number of fossils, most of which have been described by Brongniart and Meunier. The chief characteristics of the assemblage may be shortly summed up in the statement that they appear to have been at a stage when the separate Orders known to us to-day were only beginning to be foreshadowed, nearly all the specimens found being of large size, with dense wing-venation, and primitive structure of head, thorax, and abdomen. The dominant group was the Blattoidea. No undoubted Holometabolous Insects are known to exist from these beds, nor were any such known from any Palæozoic rocks, until the discovery of *Permochorista*, a genus of undoubted Mecoptera, in the Permian Coal-Measures of Newcastle, N.S.W.†

Eight species are represented in the "Mark Stirrup" Collection. Five of these are Blattoids, and one is a Palæodictyopteron. The other two are of very great interest, and their affinities are certainly problematical enough to require very careful investigation before they can be settled with anything approaching finality.

* Mem. Proc. Manchester Lit. Phil. Soc., 1916-17, Vol.61, Pt.1, No.2, pp.1-32, Pls. i.-v., [May, 1917].

† These Proceedings, 1917.

I refer to *Megagnatha odonatiformis* Bolton, and *Sycopteron symmetrica* Bolton. Bolton places the former in the family *Perlidæ* (by which the author evidently means the Order Perlaria, and not the family *Perlidæ* s.str.); though, in a note added to this determination, he states that Dr. A. D. Imms suggests that the specimen "may possibly come nearer to the *Sialidæ*," by which, I take it, he means the Order Megaloptera, rather than the actual family *Sialidæ* s.str. As for *Sycopteron*, this is assigned to the "family *Panorpidæ*," for which, again, we are evidently intended to read the "Order Mecoptera," since the author compares it with *Orthophlebia* of the Lias. If this placing be correct, then we have a Holometabolous insect present in the Upper Carboniferous—an occurrence which is, of course, not impossible, but is certainly improbable, in view of our present knowledge of the Phylogeny of the Insecta.

I have, of course, no opportunity of examining the specimens themselves; but Mr. Bolton has given us such excellent photographic reproductions and drawings of the fossils in his paper, that one would certainly scarcely desire anything better. As the determination of the affinities of these two fossils is a matter of prime importance to students of Insect Phylogeny, and as I have already informed Mr. Bolton by letter of the views that I shall here express, I propose now to state my reasons why these two insects cannot be accepted as belonging to the Orders to which Mr. Bolton would assign them, and to indicate also to what known Orders they may, with more probability, be considered to belong.

MEGAGNATHA ODONATIFORMIS Bolton. (Text-fig. 1).

Bolton, *op. cit.*, pp. 2-6, Pl. i., figs. 1-4.

From the photograph given by Bolton in Pl. i, fig. 1, and from the drawing in Fig. 3, it is evident, as Bolton himself admits, that any reconstruction of the wing-venation of this fossil must be largely a matter of conjecture. We should, therefore, attempt to find other characters that may lead to a solution. The figures show that:—

(1) The wings were either absolutely, or approximately, equal

in size, and of similar shape; probably, therefore, the venations of fore- and hindwings were the same.

(2) The insect had a small, elongated head and prothorax.

(3) The head carried a pair of straight, slender, and fairly long antennæ, and also a pair of shorter, but very prominent, somewhat curved, slender appendages, which Bolton considers, with some doubt, to have been the mandibles.

(4) The three pairs of legs were well developed, and placed far apart from one another.

(5) The abdomen was also moderately short, and probably carried two very short cerci.

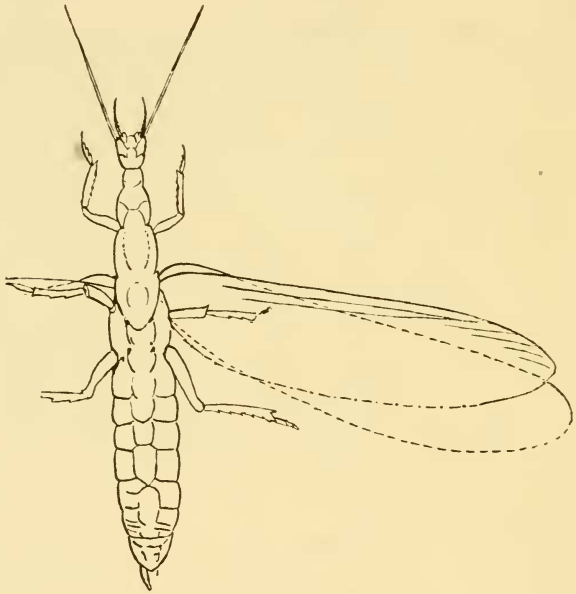
In the Perlaria, the head and prothorax are neither narrow nor elongated, but are always more or less flattened down dorso-ventrally, more or less widened; and the prothorax is never far removed from the pterothorax. The antennæ are very long, and the cerci also, in all the most archaic forms; genera in which the cerci are shortened are demonstrably descended from forms which had longer cerci. Further, fore- and hindwing are never equal in size, or of similar shape; and forms in which there is an approximation to equality are demonstrably derived from forms in which there has been greater inequality. Nor are the venations of fore- and hindwing ever the same, but differ fundamentally, as a study of the nymphal tracheation of the two wings clearly proves. Finally, the Perlaria have mostly reduced, weak, non-projecting mandibles; and it is demonstrable that these organs were never, within the limits of this Order, slender and projecting, as seen in *Megagnatha*.

Even if it were to be admitted that the restored venation in Bolton's Fig.4 were correct, I fail to see in it any true Perlarian characters. It much more resembles the venation of an archaic Termite forewing, such as *Mastotermes*.

I conclude, therefore, that no affinity between *Megagnatha* and the Order Perlaria can be shown to exist.

The only possible claim to affinity with the Order Megaloptera rests upon the projecting mandibles, since these structures also project strongly in the archaic *Corydalus* and allies. But the

mandibles of these latter insects are much more strongly built, and are attached to a broad and massive head that is as unlike that of *Megagnatha* as it well could be. We may well ask, are these "mandibular-like structures" mandibles? Is it not much more likely that they are the maxillary palpi, whose joints, like those of the antennæ, have become obscured in the fossil? They are too slender to have been of any use for biting; and sucking mandibles, such as we find in the Ant-lion, do not occur, as far as we know, in any imaginal form whatever; nor are even such sucking mandibles ever so slender as in this fossil.

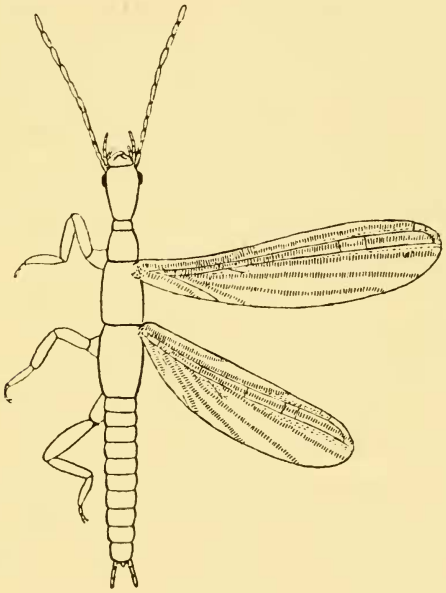


Text-fig. 1.

*Megagnatha odonatiformis* Bolton; (×42). Upper Carboniferous of Commentry. From Bolton's Pl. i., fig. 2. The short cercus on the left side of the figure is not shown in Bolton's figure, but is visible in his fig. 1 (photograph).

I am, therefore, forced again to conclude that no real affinity can be demonstrated between this fossil and the Megaloptera.

What, then, are the most likely affinities of this peculiar fossil? I should answer that it shows a very remarkable resemblance to the very ancient and mysterious Order Embioptera, about which, unfortunately, we know very little. In Text-fig. 1, I reproduce Bolton's figure of *Megagnatha*, and place opposite to it, in Text-fig. 2, a drawing of an Embid (*Oligotoma* sp., undetermined) which I happen to have in my collection. It must be at once admitted that the resemblance is a very striking one. The form of the head, prothorax, and legs, the great separation of the latter, and the equality of the wings, are characters that separate



Text-fig. 2.
*Oligotoma* sp., (undetermined) in Coll. Tillyard; (× 7½). Recent. Brisbane, Queensland.

out the Embioptera very distinctly from all other groups. All these characters are possessed by *Megagnatha*. Further, the Embioptera possess elongated maxillary palpi, which, in the position of rest, lie projecting in front of the head, much in the

manner that these supposed mandibles of *Megagnatha* do in the actual fossil. The only two discordant characters are the much more complex venation of the fossil, and the closeness of its wings at their bases. The latter may be easily explained as having been due to unequal crushing of the thorax; probably the wings were actually well separated at their bases, as the structure of the thorax, and the position of the legs, undoubtedly suggest. As for the venation, it is quite evident that recent Embioptera, like most recent Termites, possess a very reduced venation, containing only very little of the original elements. We see, in *Mastotermes*, how complex was the venation originally possessed by the Termites. In the Embioptera, the analogue of *Mastotermes* no longer exists; or, at any rate, it has not yet been discovered. But I have seen a species from Australia (of which, unfortunately, I have no notes or figures) with a venation considerably more complex than that of *Oligotoma*. All students of the Embioptera agree that they represent the last remnants of a peculiar group of great antiquity; but, so far, their fossil history has been almost completely missing.*

*Megagnatha* is larger than *Oligotoma*; but this is what we should expect, if the two are really related. For *Oligotoma* is clearly a reduced form, as its venation proves.

I would suggest, therefore, that *Megagnatha odonatiformis* is in reality an ancient representative of the Embioptera, and should be placed within that Order, as the sole known type of a new family, the *Megagnathidæ*, differing from all known members of the Order by its greater size and more complex venation, as well as, probably, by the shorter comparative distance between the bases of the fore- and hindwings.

As the identification of the "mandibular-like" structures as true mandibles is, at the best, very doubtful, and as not a single Odonate character is possessed by this fossil, it is much to be regretted that its author should have chosen a generic name

* Two doubtful records from West African Copal can scarcely be regarded as more than subfossil, and add nothing to our knowledge of the group. A single species from Baltic Amber belongs to the genus *Oligotoma*.

based upon the former character, and an entirely misleading specific name, neither of which can be altered.

Sycopteron symmetricum Bolton. (Text-fig.3, *b*, *c*).

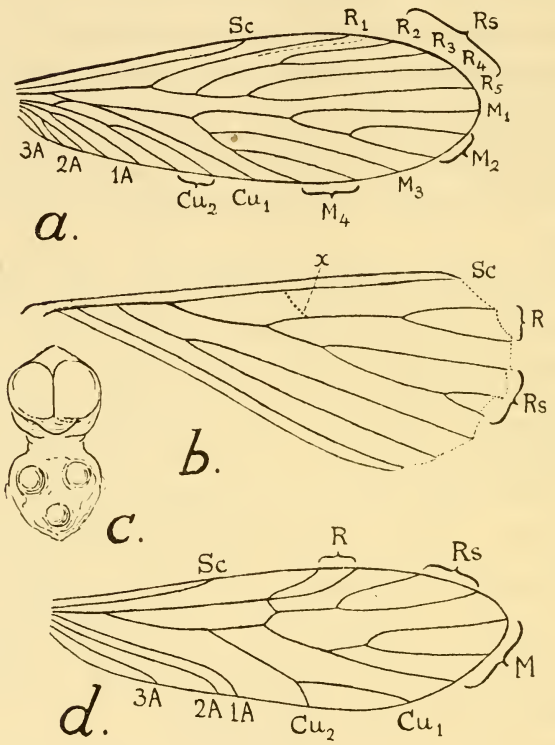
*Sycopteron symmetrica* Bolton, *op. cit.*, pp.6-8, Pl. ii., figs.1-2.

If this fossil could be proved to be Mecopterous, it would be one of the most striking discoveries in Palæoentomology. For that reason alone, we are all the more bound to examine the evidences of its supposed Mecopterous affinities as carefully as possible.

Text-fig.3, *b*, *c*, are portions of Bolton's Pl. ii., fig.2, which, as far as I can see by comparison with the photograph in his fig.1, is accurate in all except a possible minor detail or two. The first thing that strikes one, on examining this fossil, is the way that its wings are folded down the back of its abdomen. If this were the natural position of rest, it would be that of a Dipteron or a Hymenopteron; yet both these Orders are excluded from the question, for reasons that must be sufficiently obvious without stating them. We have, then, to conclude, either that *Sycopteron* belonged to some extinct Order, which folded its wings in this position (a highly improbable theory), or that it belonged to some Order in which the wings were held roof-like over the abdomen; in which case, the flattening down of the wings in the fossil may well have caused some underfolding of either the costal or the posterior border of the wings, or both.

Bolton claims for his insect a Panorpoid venation, stating that its nearest approach is to be found in *Orthophlebia* of the Lias. When, however, he goes into detail, it is quite clear that he is unable to homologise the separate veins of *Sycopteron* with those of *Orthophlebia*, without getting into very serious difficulties. In order to show this, I give in Text-fig.3, *a*, *b*, the venation of *Sycopteron*, (*b*), as interpreted by Bolton, and the venation of *Permochorista*, (*a*), which is the oldest fossil Mecopteron known, and the venation of which closely resembles that of *Orthophlebia*. It will be seen at once that the type of venation present in the Mecoptera (and there is no Order in which the venation is more

constant in character, differing little right through from the Permian to recent times) is radically different from that of




Text-fig.3.

*a*, Forewing of *Permochorista mitchelli* Tillyard, (restoration, with all the cross-veins omitted); (×4). Permian of Newcastle, N.S.W. *b*, Forewing of *Sycopteron symmetricum* Bolton, with his naming of the veins; (×$7\frac{3}{4}$). Upper Carboniferous of Commentry. From Bolton's Pl. ii., fig.2. *c*, Head and thorax of same, from the author's same figure; (×$7\frac{3}{4}$). *d*, Forewing of *Amphientomum paradoxum* Br.; (×15). Oligocene, Baltic Amber. From Enderlein. In *b*, the dotted vein *x* indicates the probable position of the basal piece of Rs, not shown in Bolton's fig.2, but apparently slightly indicated in his fig.1 (photograph).

*Sycopteron*, this latter being of a much simpler type, which does not occur in the Order Mecoptera at all. The resemblance is

due only to the method of branching dichotomously, and the absence of clearly-marked crossveins,—characters which are by no means confined to the Mecoptera.

I would suggest that the true costa of this insect has become folded under in the fossil, and is not clearly visible. Bolton says, "The costal margin seems to have been extremely delicate, and to have left very faint traces of its position." This might well be true of the subcosta, which is frequently a weak vein. In the Mecoptera, the costa is strongly formed, but there are other insects in which it is not so. This suggestion receives support from the fact that, if the front vein preserved in this fossil is really the costa, then Sc, R, and M all come off from a common stem, in a manner that cannot be paralleled except in the Homoptera, and certainly never occurs in the Mecoptera.

Whether we allow that the costa was underfolded or not, the following dilemma has to be faced:—

(1) If the fossil is Mecopterous, then the naming of the veins by Bolton is incorrect. The five-branched vein which he has distributed between R and Rs is certainly the media; and we are then driven to suppose that all the rest of the venation, costad of this, has been underfolded, except a portion of Rs, which would be Bolton's Sc.

(2) If Bolton's naming of the veins is correct [or even if the large extent of underfolding suggested in (1) cannot be admitted], the fossil is neither Mecopterous, nor in any way related to the Mecoptera, since the typical Sc, R, and Rs of that Order—the latter alone of which is never less than four-branched*—are all absent.

From this dilemma, there is only one escape, viz., to admit at once that the Mecopterous affinities, much as we must regret it, cannot be proved, and to seek for some more likely solution of the problem.

In Text-fig.3, *d*, I show the venation of the forewing of the very archaic insect *Amphientomum paradoxum* Br., from Baltic

* Excepting in the highly reduced, recent *Nannochoristidæ*, where it is three-branched.

Amber. This insect belongs to the Order Psocoptera or Copeognatha, an Order which is not Holometabolous, but which possesses a reduced venation very closely resembling that of certain Holometabolous Orders, in particular the Hymenoptera. Nearly all recent Psocoptera have a much more specialised venation than *Amphientomum*; but close relatives of the latter still exist in the peculiar genera *Echmepteryx* and *Cymatopsocus*, as well as the genus *Amphientomum* itself, which has recently been rediscovered in Ceylon.

It will be seen that the correspondence between the wing-veins of *Sycopteron* and *Amphientomum* is exceedingly close; in fact, they can be completely homologised, provided only that *Sycopteron* possesses the short basal piece of Rs which is absent from Bolton's figure. A close examination of the photograph of *Sycopteron*, in Bolton's Pl. ii., fig. 1, suggests to me that this piece actually does exist; at any rate, it seems to be clearly indicated on the left wing. The fossil should certainly be further examined to determine this point.

In *Amphientomum*, the subcosta is a very weak vein, merging into the costa before halfway. The radius is a strong vein, forked distally, and giving off its sector far distally, at a point only just before its fork. Rs itself is forked, as in *Sycopteron* (the vein Bolton calls R). Further, M is three-branched in *Amphientomum*, in the same manner as in *Sycopteron* (the vein Bolton calls Rs). In *Amphientomum*, the cubitus is forked far distad, and is attached to the stem of M at a point quite one-third of the wing-length from the base; in *Sycopteron*, the attachment and forking lie both much further basad. So also the anal veins in *Amphientomum* are less primitive than in *Sycopteron*, being shorter and less straight.

Now *Amphientomum* is evidently specialised in the following points:—

(1) The shortening of Sc.

(2) The removal of the origin of Rs far distad, and consequent shortening of that vein.

(3) The close union basally between M and Cu.

(4) The removal of the cubital fork far distad.

(5) The shortening and curvature of the anal veins.

If, then, ancestors of this insect existed in Palæozoic strata, we should expect them to exhibit a generalised condition in these five characters. This is exactly what *Sycopteron* does exhibit. Without stating positively that *Sycopteron* lies in the ancestral line of *Amphientomum*, yet we can affirm that, as far as its venation is concerned, the two are certainly closely allied, and *Sycopteron is the older type*.

Let us now examine the rest of the fossil for clues as to its affinities. The first peculiarity to be noted is the huge boss-like areas upon the back of the head (Text-fig.3, *c*). If these be compound eyes, then *Sycopteron* is certainly neither a Mecopterous nor a Psocopterous insect; but, as Bolton mentions no facets on these areas, we may confidently take it that they are not. They must, therefore, be epicranial or occipital swellings. Now the head of *Sycopteron* is much too prominently developed to agree with the Mecopterous type. But almost all the Psocoptera have a comparatively large head, with prominent development of the posterior portion of the epicranium. If such a head were to be crushed somewhat in becoming fossilised, its appearance would certainly closely resemble that of *Sycopteron*. The small eyes would probably be completely covered by the flattened epicranium.

The structure of the thorax in *Sycopteron* is certainly primitive, and might indicate equally well affinities with several Orders, including both Psocoptera and Mecoptera (Text-fig.3, *c*).

Again, in the Psocoptera, the hindwing is always small and weakly chitinised. Hence, in insects of this Order which might become fossilised with their wings flattened down over the abdomen, no sign of the hindwing or of its venation would appear. The Mecoptera, on the other hand, have, of all the insects, except the Odonata and Planipennia, the most strongly chitinised hindwings, of a size almost equal to the forewings, and with a strongly marked and closely similar venation. Hence, if a Mecopteron became fossilised in the position we are supposing, it seems inevitable that traces of the hindwings and of their main veins

must be present. But Bolton mentions nothing of this sort, and the photograph in his Pl. ii., fig. 1, certainly shows nothing that could be so interpreted. The probability, then, of this fossil having belonged to the Mecoptera, is very much diminished upon this count alone

Taking all the evidence into consideration, it seems legitimate to conclude that *Sycopteron* is most certainly not a member of the Order Mecoptera, but that it is very likely an archaic type of the Order Psocoptera, related to *Amphientomum* of the Oligocene, but considerably less specialised, in that it lacks all five of the venational specialisations possessed by this genus. It should certainly be placed in a new family *Sycopteridæ*, having the characters already mentioned. It should be noticed that the size of this insect (wings 9-10 mm.) agrees very well with its inclusion in the Order Psocoptera, all the known members of which are small, ranging from a wing-length of only 10 mm., at most, down to very minute and wingless recent forms.